APOGAMY IN THE CYATHEACEAE

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(WITH TEN FIGURES)

Since the discovery of apogamy in *Pteris cretica* by FARLOW (3) in 1874, it has been observed in about 15 genera and 30 species of the Polypodiaceae. There are records of its occurrence in 3 other families of the Filicales, namely, the Osmundaceae, the Hymenophyllaceae, and the Marsiliaceae. It has been reported by SADEBECK (9) in *Todea africana*, by LEITGEB (7) in *Osmunda regalis*, by STANGE (12) in *Todea rivularis* and *T. pellucida*, by BOWER (1) in *Trichomanes alatum*, by WORONIN (14) in *Trichomanes Krausii*, and by SHAW (11) and STRASBURGER (13) in *Marsilia*.

For several years I have been making a study of the prothallia of the Cyatheaceae, most of the results of which will appear in a later paper. I have had under cultivation 13 species belonging to 5 of the 7 genera. The species studied include 6 species of *Alsophila*, 1 of *Hemitelia*, 2 of *Cyathea*, 2 of *Dicksonia*, and 2 of *Cibotium*. I am indebted to Dr. J. M. GREENMAN for the determination of all the species with the exception of *Alsophila Cooperi* F. Muell., which was obtained from the greenhouses of Harvard University, and *Cyathea muricata* Wild. (*Alsophila muricata* Desv.), obtained from the New York Botanical Garden.

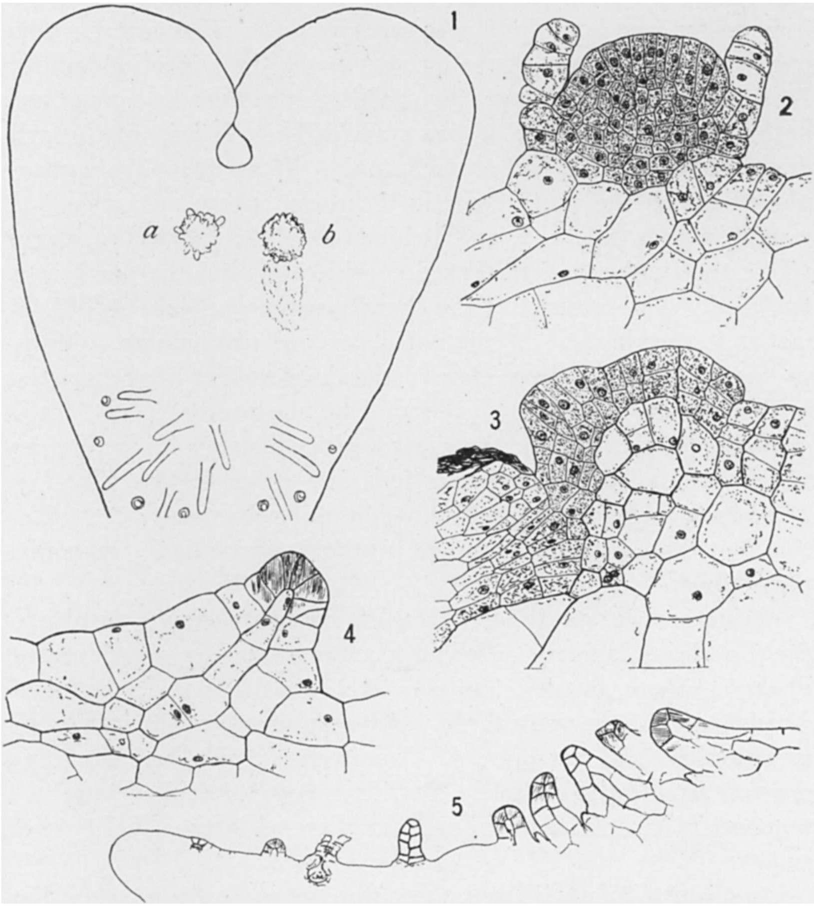
In order to obtain pure cultures it was found necessary to take measures to remove foreign spores from material obtained from greenhouses where other ferns were growing. The leaves, which were collected before the sporangia had begun to open, were washed in running water and brushed rather vigorously while in the water. They were dried on sterilized glass plates and the spores which were collected were sowed on various culture media. Cultures from material handled in this way contain few if any foreign prothallia. It is not difficult to tell by the appearance of a culture whether or not there are any foreign prothallia present, owing to differences in the rate of development and in the general habit of the prothallia of different species. It is fairly easy to distinguish between the

prothallia of the Polypodiaceae and the Cyatheaceae because of the differences in the antheridia and in the types of hairs.

From 2 to 15 cultures were made of all the species studied, the cultures running from 5 to 15 months. Various media were used: several different mixtures of soil; black peat, with and without Knop's solution; and porous clay crock standing in Knop's solution. Some of the cultures were raised in a laboratory where they received no direct sunlight except late in the afternoon; others were raised in a greenhouse where they received sunlight except for a few hours at midday.

The few cases of apogamy found occurred in the genera *Dicksonia* and *Cyathea*. They were found in cultures on peat raised in the greenhouse in the winter of 1915–1916. I am indebted to Professor A. VINCENT OSMUN of the Massachusetts Agricultural College for data on the weather of that winter and the 5 years preceding. While the total number of hours of sunlight for the winter of 1915–1916 was a little below the average, the number of days in which there was snow on the ground was considerably above the average, so that the greenhouse cultures of that winter probably received more light than any other set of cultures. LANG (8) regards intense light and probably high temperature as important factors in the development of apogamous structures. SCHLUMBERGER (10) found that in the case of *Woodsia ilvensis* the production of the cylindrical process was caused by such unfavorable conditions as weak light and dryness. HEILBRON (4) did not find dryness to be a factor and suggests that summer cultures are more likely to become apogamous than winter cultures, but his experiments with different qualities and intensities of light in moist cultures at a high temperature gave negative results. Mme. WORONIN is inclined to regard dryness as the cause of apogamy in the forms which she studied, as in these cases it cannot be attributed to intense light. This explanation is criticized by ISABURO-NAGAI (6), who found that in the case of *Asplenium Nidus* dryness was not a factor and that the cause seemed to be either an unfavorable culture condition or an unknown physiological condition. The cases discussed in the present paper are too few in number to be of much significance. It cannot be a question of dryness, as the cultures were on

moist peat. They were, however, exposed to rather intense light. It seems to be true that one explanation will not answer for all cases; the factors which cause apogamy in *Woodsia ilvensis*, a



FIGS. 1–3, 5.—*Dicksonia squarrosa:* fig. 1, prothallium with two apogamous buds, ×22; fig. 2, section through *a*, ×210; fig. 3, section through *b*, ×210; fig. 5, section of prothallium with archegonia and archegonial projections, ×90. Fig. 4, *Cyathea Tussacii:* archegonial projection, ×170.

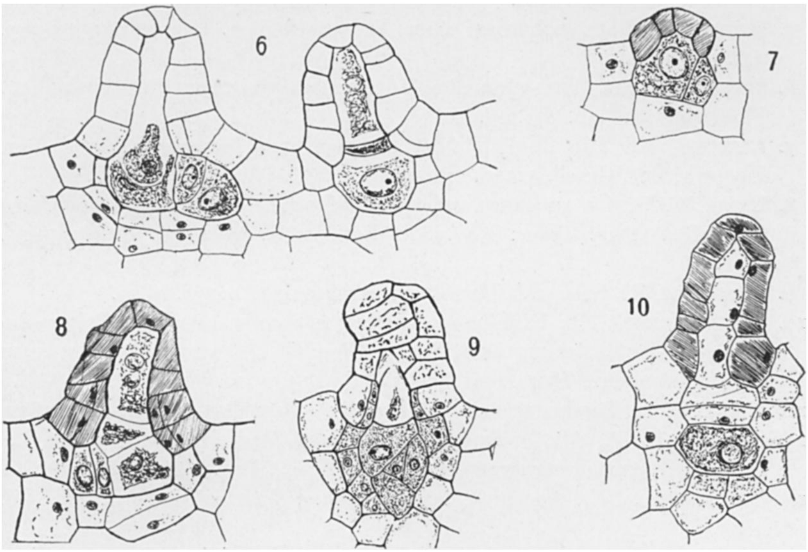
species which grows in exposed situations, are not necessarily the same as those which cause it in the species which grow in shaded places.

A convenient classification of types of apogamous development has been presented by FARMER and DIGBY (2), who begin their classification by distinguishing between premeiotic and postmeiotic apogamy. All the prothallia described in this paper were raised from spores, and accordingly the cases would be postmeiotic. The only case of obligate apogamy was found in a prothallium of *Dicksonia squarrosa* (Forst.) Sw. This prothallium had numerous antheridia and, although it was sufficiently large and had a well developed cushion, it had no archegonia. It produced two apogamous buds on the ventral side in the region where the archegonia usually appear (figs. 1, 2, 3). Behind one of the buds was a region where the thallus had thickened considerably and the outer cells had died. The presence of the characteristic cyatheoid antheridia makes it certain that this is not a polypod prothallium. Many prothallia of *D. squarrosa* showed the development of archegonial projections, such as HEIM (5) found on the prothallia of *Doodia caudata* and LANG found associated with apogamy in the species which he studied. Such projections are shown in figs. 4 and 5. *D. squarrosa* sometimes produced embryos as the result of fertilization, but these were not found on prothallia which had archegonial projections.

Cyathea muricata Wild. (*Alsophila muricata* Desv.) furnished the case shown in fig. 9. This may be the apogamous development of the oosphere, but it is quite as likely that it is the apogamous development of the ventral cell. Adjoining sections show that the archegonium had not opened. A nutritive region had begun to develop around the embryo. It will be noted that the shape and sequence of cell divisions are not the same as in the usual type of embryo.

In *Cyathea Tussacii* Desv. there were several cases of a peculiar behavior of the central cell. The first division does not cut off the primary neck cell, but instead cuts off a lateral cell (fig. 7). The central cell develops in the usual manner, while the lateral cell develops such structures as are seen in figs. 6 and 8. Such a division in the central cell was found also in *Dicksonia squarrosa* and a single case occurred in *Cibotium Schiedei* Schlecht. and Cham. *Cyathea Tussacii* and *Cibotium Schiedei* both produced archegonial

projections. In *Hemitelia horrida* (L.) R. Br. occurred the peculiar structure shown in fig. 10, an archegonium in which all the cells of the axial row except the egg have developed as vegetative tissue. The only development possible in this case would be an apogamous development. This species, however, showed no tendencies in that direction. It is impossible to say whether or not such structures as those shown in figs. 6, 7, 8, and 9 ever produce leafy



FIGS. 6–8.—*Cyathea Tussacii:* explanation in text, ×255; fig. 9, apogamous embryo of *Cyathea muricata*, ×255; fig. 10, peculiar archegonium of *Hemitelia horrida*, ×220.

sporophytes, as in a very short time it would be impossible to distinguish such an embryo from one produced as the result of fertilization. There was nothing in any of the material to indicate that these growths were ultimately checked, but the cultures did not continue long enough to show whether or not they would develop further. Neither species of *Cyathea* produced any embryos as a result of fertilization, although most of the archegonia appeared normal and the sperms were active, many being found in archegonia.

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